THE FORAMINIFERID GENUS *GAVELINELLA* IN THE SENONIAN OF NORTH-WEST EUROPE

by P. G. EDWARDS

ABSTRACT. The morphology and stratigraphic importance of species, subspecies and varieties of the genus *Gavelinella* from the Senonian (Upper Cretaceous) chalk of north-west Europe are discussed. It is suggested that several stratigraphically significant lineages arose from a *Gavelinella schloenbachi* (Reuss) ancestor during the Senonian. Within the *Gavelinella clementiana* (d'Orbigny) plexus of evolving forms, one subspecies *G. clementiana convexa* is described as new. The *Gavelinella lorneiana* (d'Orbigny)–*G. pertusa* (Marsson) lineage is regarded separately, and it is suggested to have arisen from a *Gavelinella ammonoides* (Reuss) ancestor during the Turonian.

PROGRESSIVE changes observed in faunas may be used as indices of time. If the direction of these changes can be deduced, then the lineage(s) can be used to better advantage biostratigraphically than if only an occasional individual is observed.

With reference to the information gained from the studied sections, and from an extensive survey of the available literature, the author reinterprets the rudimentary evolutionary schemes erected by Brotzen (1942) and Hiltermann and Koch (1960); and the more comprehensive schemes of Bulgarian and Soviet workers (Vassilenko 1954; Vaptzarova 1970).

A total of 200 samples were examined from southern England, East Anglia, and northern France (text-fig. 1) of which 180 were analysed numerically, the remainder being in the form of mounted assemblage slides which were made available to the writer by Professor D. Curry. The scope of the study was extended through the compilation and assimilation of information contained in the major works relating to European Senonian foraminifera: Brotzen (1945); Hiltermann and Koch (1960); Hofker (1949, 1951, 1956, 1958–1959); Kaptarenko-Chernousova *et al.* (1963); Koch (1973, 1975, 1977); Marie (1941); Schijfsma (1946); and Vaptzarova (1970), which cover northern Germany, Belgium, the Netherlands, Sweden, France, Bulgaria, and the U.S.S.R.

Deposition of types. The holotype and paratypes of *Gavelinella clementiana convexa* are deposited in the British Museum (Natural History), London, together with all the hypotypes illustrated in this paper. The index numbers allocated to these specimens are given in the plate descriptions. All other paratypes and additional material are housed in the collections of the Department of Geology (Micropalaeontology), University College, London.

TERMINOLOGY OF SENONIAN STRATA

In order that the stratigraphic distribution of the gavelinellids outlined in this study may be expressed without ambiguity, it is necessary to standardize the stratigraphy (Table 1). The subdivisions employed during the present study are in accordance with those outlined in the most recent published account of the Cretaceous rocks of the British Isles (Rawson *et al.* 1978, pp. 22–29). The lowermost limit of the Santonian stage has not been well-defined, and is subject to much disagreement between the various workers. The author favours the placement of the Coniacian–Santonian stage boundary towards the top of the *Micraster coranguinum* zone as defined by the uppermost stratigraphic limit of *Gavelinella vombensis* (Brotzen)—a scheme also employed by Gigout and Monciardini (1976). This datum level is more precise than that marking the disappearance of *Gavelinella praeinfrasantonica* (Vassilenko and Myatliuk) in that the latter grades into *G. infrasantonica* (Balakhmatova) (= *G. vombensis*) through a series of transitional forms.

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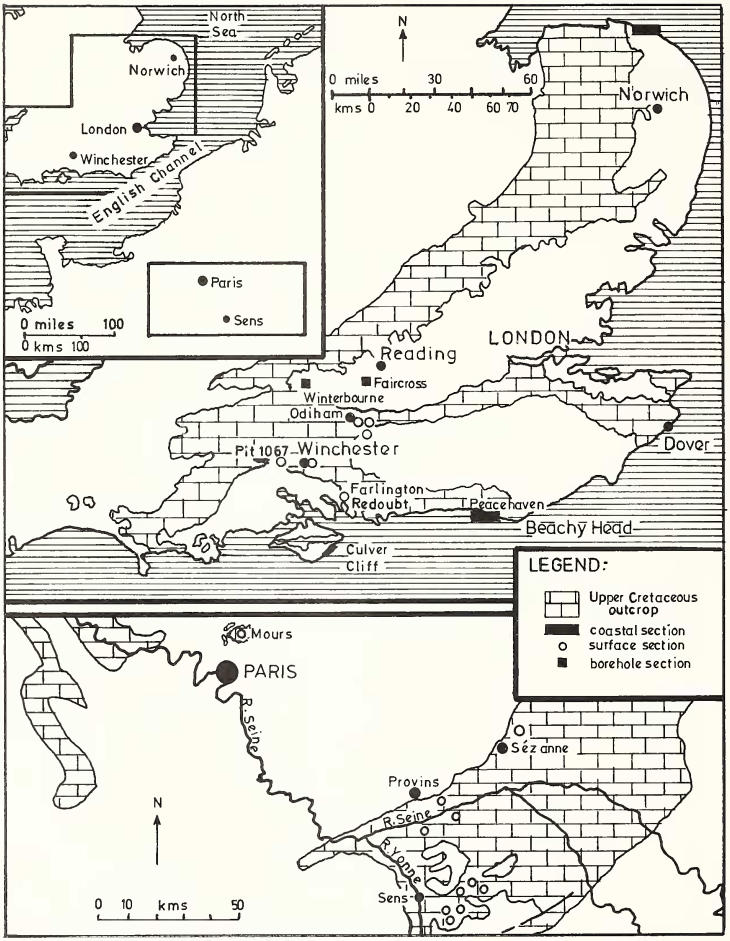


TEXT-FIG. 1. The geographic location of sample localities in relation to the Upper Cretaceous outcrop.

SERIES	STAGE (Coquand, 1856)		ZONE: BRITAIN: Rawson* et.al., 1978.	ZONE: FRANCE: Conventional ammonite zone (de Grossouvre, 1895-1901.)	ZONE: FRANCE: Barrois, 1876	ZONE: FRANCE: Arnaud, 1878, 1883.	ZONE: FRANCE: Stokes, 1975.	GERMAN STAGES
UPPER CRETACEOUS	LOWER MAESTR-ICHTIAN		*Belemnella lanceolata*	*P.neubergicus*		Q	*B.lanceolata*	MUCRONATEN SENON
	SENONIAN (d'Orbigny, 1840)	CAMPANIAN	*Belemnitella mucronata*	*B.polyplocum*	Craie à *B.mucronata*	P3	*B.mucronata*	
				H.vari				
			Gonioteuthis quadrata	*M.delawar--ensis.*	Craie à *B.quadrata*	P2	*Actinocamax quadratus*	QUADRATEN SENON
			Offaster pilula	*D.bidorsatum*		P1		GRANULATEN SENON
		SANTONIAN	*Marsupites testudinarius*	*P.syrtale*	Craie à Marsupites	N2	*M.coranguinum*	EMSCHER
						N1		
			Uintacrinus socialis	*T.texanus*		M2		
						M1		
		CONIACIAN	*Micraster coranguinum*	*P.emscheris*	Craie à I.involutus	L2	*M. decipiens*	
						L1		
			Micraster cortestud--inarium	*B.haberfell--neri.*	Craie à *M.cortestud--inarium.*	K		
	UPPER TURONIAN		*Holaster planus*	*S.neptuni*	*E.brevis*		*M.normanniae*	

Craie à *M.coranguinum*

TABLE 1. Correlation of some Senonian biostratigraphic subdivisions based on macrofossils (* scheme employed by the author).

SYSTEMATICS

The writer employs the classificatory scheme outlined by Loeblich and Tappan (1964, 1974). With the exception of the newly described subspecies *G. clementiana convexa*, the present author does not provide a full morphological description of the species, subspecies, and varieties outlined, but instead refers the reader to the original descriptions quoted in the synonymy lists.

Kingdom PROTISTA
Phylum PROTOZOA
Order FORAMINIFERIDA
Suborder ROTALIINA
Superfamily NONIONACEA
(nom. transl. Subbotina, 1959, ex subfamily)
Family ANOMALINIDAE
Genus GAVELINELLA
(= *Pseudovalvulineria* Brotzen, 1942, and *Anomalina* (*Brotzenella*) Vassilenko, 1958).

The presence of an umbilical knob and a less open umbilicus has been used to distinguish the genus *Pseudovalvulineria* from the genus *Gavelinella*. Loeblich and Tappan (1964) suggested that these distinguishing characteristics are not constant, and are subject to considerable variation. The apertural features are identical, hence *Pseudovalvulineria* is here regarded as a synonym.

Gavelinella clementiana (d'Orbigny)

Remarks. The *G. clementiana* species group, ranges from the base of the *Gonioteuthis quadrata* zone to the top of the *Belemnitella mucronata* zone. Marie (1941, p. 212, pl. 33, figs. 309–313) recognized a number of morphologically distinguishable forms which he described in terms of varieties. The writer is in agreement with this division but applies a sub-specific status to Marie's varieties on the basis that they can be separated both morphologically and stratigraphically.

Gavelinella clementiana clementiana (d'Orbigny)

Plate 58, figs. 3–5

1840 *Rosalina clementiana* d'Orbigny, p. 37, pl. 3, figs. 23–25.
1870 ?*Rotalia fontana* Karrer, p. 184, pl. 11, fig. 16.
1931 ?*Anomalina clementiana* (d'Orbigny); Cushman, p. 61, pl. XIII, fig. 1*a–c*.
1934 *Anomalina clementiana* (d'Orbigny); Dain, p. 45, pl. 5, fig. 48*a–c*.
1941 *Discorbis clementiana* (d'Orbigny) forma *typica* Marie, p. 213, pl. 33, fig. 312*a–c*.
1946 *Discorbis clementiana* (d'Orbigny); Schijfsma, pp. 81, 82, pl. 4, fig. 11*a–c*.
1957 *Anomalina pseudoexcolata* Kalinin; McGugan, pp. 343, 344, pl. 32, fig. 22*a*, *b*.
1960 *Gavelinella clementiana* (d'Orbigny); Hiltermann and Koch, p. 71, table 2.
1961 *Gavelinella clementiana* (d'Orbigny); Barr, pp. 307–310, pl. 20, fig. 1*a–c*.

Remarks. This represents the nominate subspecies equivalent to the type *Rosalina clementiana* of d'Orbigny (1840) and to *Discorbis clementiana* forma *typica* of Marie (1941). The ornamentation on the surface of the low trochospiral test is significantly coarser, but not as extensively developed as in *G. pseudoexcolata*.

Stratigraphic range. *Belemnitella minor* sub-zone (*B. mucronata* zone) to the top of the Campanian. The author records this subspecies in the Weybourn and Paramoudra chalks of the north Norfolk coastal section and in the *B. mucronata* zone (uppermost Campanian) of the section at Mours in the Paris Basin. The specimens recovered from north Norfolk are comparable with those figured by Hofker (1956) from the Craie de Nouvelles of Belgium which Peake and Hancock (1970) recognize as the lateral equivalent of the Weybourne chalk.

Gavelinella clementiana convexa n. ssp.

Plate 57, figs. 9–13

1960 *Gavelinella clementiana* (d'Orbigny); Hiltermann and Koch, pp. 321–322, pl. 48, fig. 5.
1945 *Pseudovalvulineria vombensis* Brotzen (pars), p. 50, text-figs. 1–4.
1961 *Cibicides denticulata* Marie; Barr, pp. 411–413, pl. 34, figs. 1*a–c*, 2*a–c*.
1965 *Pseudovalvulineria eva* Goel. p. 196, pl. 13, fig. 1*a–c*.
1965 *Pseudovalvulineria glabra* Goel, p. 202, pl. 14, fig. 2*a–c*.
1965 *Gavelinopsis trochus* Goel, p. 206, pl. 15, fig. 1*a–c*.
non 1941 *Cibicides voltziana* (d'Orbigny) var. *denticulata* Marie, p. 248, pl. 37, figs. 348*a–c*, 349*a–c*.

Diagnosis. The central area of the strongly convex dorsal surface is occupied by a mass of thickened shell material of variable size, which obscures the early whorls.

Description. Test free, trochospiral, consisting of three whorls. Dorsal side strongly convex, involute early whorls obscured by a thickened mass of shell material. The ventral side of the test is slightly convex, involute, with a central umbilical plug formed by extensive thickening of clear shell material along the spiral suture. The periphery in equatorial view is circular, slightly indented between the last-formed chambers. The periphery in end view is acutely rounded. The chambers in the early whorls are indistinct becoming clearly defined in the final whorl. There are eight to ten weakly inflated chambers in the final whorl, uniformly and gradually increasing in size. The dorsal sutures are indistinct, limbate, oblique, slightly raised becoming weakly depressed in the final portion of the test. The ventral sutures are distinct, gently curved, radial, bordered or covered by a raised ridge in the early part of the final whorl. The ventral septal ridges become swollen and fused proximally. The aperture is a broad, low arch on the ventral side of the inner margin of the final chamber, with a slit-like extension into the umbilical area. The wall is calcareous, finely perforate dorsally, coarsely perforate ventrally.

Dimensions of holotype. Maximum diameter 600 μm; maximum thickness 400 μm.

Remarks. This subspecies is distinguished from *G. clementiana clementiana* by having a well-developed dorsal calcitic mass occupying the central area of the test, and by not possessing imperforate portici covering the ventral umbilicus. *Cibicides denticulata* Marie, as identified by Barr (1961), is the same as *G. clementiana convexa* of the present author. Barr cited his figured specimens as coming from samples C18 and C19, close to the *Gonioteuthis quadrata–B. mucronata* zonal junction in the chalk of the Isle of Wight, England. Analysis of Barr's specimens shows that they differ from Marie's type figure for *Cibicides voltziana* (d'Orbigny) var. *denticulata* in having tangential dorsal sutures and bearing dorsal ornamentation.

Goel (1965) set up several new species assigned to the genus *Pseudovalvulineria* within the *Gonioteuthis quadrata* zone of the Upper Cretaceous of the Seine Basin, France, which, in the writer's opinion represent specimens showing various stages in the development of *Gavelinella clementiana convexa*. Since Goel's species are not stratigraphically distinct, they are herein regarded as being synonymous and are included in the synonymy for *G. clementiana convexa*.

Holotype—B.M. index. P50795.

Paratypes—B.M. index. P50796, P50797.

Type level—*Gonioteuthis quadrata* zone.

Type locality—Brydone's Pit 1067, Hampshire, southern England (Brydone 1912), sample number 1067/3, 39·5 m above the base of the section.

Stratigraphic range. Base of the *Gonioteuthis quadrata* zone to the lowermost horizons of the *B. mucronata* zone.

Localities. 2, 3, 4, 18. (For list of localities see pp. 43–45)

Gavelinella clementiana costata (Marie)

Plate 57, figs. 14–16; Plate 58, figs. 1, 2

1941 *Discorbis clementiana* (d'Orbigny) var. *costata* Marie, p. 214, pl. 33, figs. 313*a–c*.
1977 *Gavelinella clementiana* (d'Orbigny); Koch, p. 46, pl. 2, figs. 4–6.

Remarks. This subspecies is distinguished from *G. clementiana clementiana* in possessing a greater degree of dorsal ornamentation in the form of raised septal ridges. *G. clementiana costata* represents the transitional stage, morphologically, between *G. clementiana convexa* and *G. clementiana clementiana*.

Stratigraphic range. Base to the top of the *B. mucronata* zone.

Localities. 1, 2, 20, 21.

Gavelinella clementiana laevigata (Marie)

Plate 58, fig. 6

1941 *Discorbis clementiana* (d'Orbigny) var. *laevigata* Marie, p. 212, pl. 33, fig. 309*a–c*.
1954 *Anomalina* (*Pseudovalvulineria*) *clementiana laevigata* (Marie); Vassilenko, p. 92, pl. 10, fig. 2.
1972 *Gavelinella laevigata* (Marie); Hanzlikova, p. 131, pl. 39, fig. 1.

Remarks. This subspecies is characterized by the dorsally unornamented nature of the test.

Stratigraphic range. *B. minor* subzone to the top of the *B. langei* sub-zone, within the *B. mucronata* zone.

Localities. 1, 22.

Gavelinella lorneiana (d'Orbigny) *sensu stricto*

Plate 56, fig. 1–5

1840 *Rosalina lorneiana* d'Orbigny, p. 36, pl. 3, figs. 20–22.
1845 *Discorbina lorneiana* (d'Orbigny); Reuss, p. 456, no figs.
1880 *Anomalina rudis* (Reuss); Berthelin, p. 68, pl. IV. fig. 15.
1899 (1902) *?Anomalina monoliliformis* (Reuss); Egger, p. 153, pl. XVIII, figs. 16–18.
1909 *Anomalina* (*Rosalina*) *lorneiana* (d'Orbigny); Egger, p. 45, pl. IV, figs. 10–12.
1931 *Anomalina clementiana* (d'Orbigny); Cushman, p. 46, pl. 6, fig. 10*a–c*.
1941 *Discorbis lorneiana* (d'Orbigny) Marie, pp. 214–216, pl. 33, fig. 314*a–c*; pl. 34, fig. 315*a–c*.
1941 *Discorbis lorneiana* (d'Orbigny) var. *costulata* Marie, p. 216, pl. 34, fig. 315*a–c*.
1946 *Anomalina clementiana* (d'Orbigny); Cushman, p. 155, pl. 63, figs. 12, 13.
1954 *Anomalina clementiana* (d'Orbigny); Frizzell, p. 130, pl. 21, fig. 2*a–c*.

Remarks. *Gavelinella lorneiana sensu stricto* is characterized by its low, trochospirally coiled test with a sub-circular periphery. The septal ridges are gently curved, and on the ventral surface of the test project into the umbilicus. The ventral ridges are separated by coarsely perforated areas. The final chamber varies in the degree of its inflation.

Discorbis lorneiana var. *costulata* differs from Marie's typical *D. lorneiana* in possessing well-defined septal/sutural ridges dorsally; a greater number of chambers (thirteen in the final whorl); a less-inflated apertural face, and in the presence of a dorsal umbilical boss. In the writer's opinion, these features are subject to variation, and show no definite trends through time. The prominence of the septal ridges appears to be a function of their degree of broadening and flattening. Broad, smoothly convex septal ridges give the appearance of inflated, imperforate chambers, thus obscuring the actual number of chambers present. The writer therefore includes *D. lorneiana* var. *costulata* in the synonymy for *G. lorneiana sensu stricto*.

Brotzen's (1942, p. 47 fig. 15) figured specimens of *Gavelinella tumida* resemble d'Orbigny's *Rosalina lorneiana* in many respects, but differ from the latter in possessing a deeper umbilicus, and in

the absence of septal ridges. Brotzen's figures illustrate the degree of variation in the size and inflation of the final chamber, as observed in specimens of *G. lorneiana sensu stricto* studied by the writer. The present author suggests that the apparent absence of septal ridges in Brotzen's figured specimens of *G. tumida* may be due to their excessive flattening and coalescing so that they become indistinguishable from true chambers. This broadening of the imperforate septal ridges would tend to obscure the interspersed perforate areas—Brotzen's specimens appear to lack coarsely perforate chamber walls. However, examination of Brotzen's type material is necessary in order to determine the actual character of the test morphology. Until such an examination is carried out, the writer prefers not to include *G. tumida* in the synonymy for *G. lorneiana sensu stricto*.

Stratigraphic range. *Holaster planus* zone (topmost Turonian) to the *B. minor* sub-zone (*B. mucronata* zone, Upper Campanian)

Localities. 2–21.

Gavelinella lorneiana (d'Orbigny) var. *A*

Plate 56, fig. 6

Remarks. This variety differs from *G. lorneiana sensu stricto* only in the presence of lateral elongations flanking the apertural face, giving the final chamber a more acute periphery. These elongations are formed by the curved sutural ridges bordering the last-formed chamber. However, *G. lorneiana* var. *A* is neither stratigraphically nor geographically distinct from *G. lorneiana sensu stricto*, therefore the latter is not given a sub-specific status.

Gavelinella monterelensis (Marie)

Plate 58, figs. 15–17

1941 *Anomalina monterelensis* Marie, p. 243, pl. 37, fig. 342*a–c*.
1946 *Anomalina menneri* Keller, p. 103, pl. 1, figs. 14–16; pl. 3, figs. 16, 17.
1946 *Cibicides voltziana* (d'Orbigny) var. *plana* Schijfsma, p. 104, pl. 5, fig. 7*a–c*.
1954 *Anomalina* (*Pseudovalvulineria*) *monterelensis* Marie; Vassilenko, p. 108, pl. 16, figs. 5, 6.
1957 *Gavelinopsis menneri* (Keller); Hofker, p. 333, text-figs. 385, 386.
1961 *Cibicides plana* Schijfsma; Barr, pp. 413–415, pl. 34, figs. 3*a–c*, 4*a–c*.
1964 *Gavelinella monterelensis* (Marie); Loeblich and Tappan, p. C759, fig. 621*a–c*.
1970 *Anomalina* (*Brotzenella*) *monterelensis* Marie; Vaptzarova, p. 61, text-fig. 3.

Remarks. Loeblich and Tappan (1964) assigned *Anomalina monterelensis* Marie to the genus *Gavelinella* on the basis of apertural configuration. The type figure for *C. voltziana* var. *plana* differs from the type *A. monterelensis* only in the less inflated final chamber, which gives the apertural face a more acute periphery, and in the less pronounced ventral septal ridges. These forms otherwise show a strong morphological similarity and corresponding stratigraphical ranges, and are herein regarded as being synonymous.

Stratigraphic range. Upper part of the *Gonioteuthis quadrata* zone to the uppermost part of the *B. mucronata* zone.

Localities. 1, 2, 3, 20, 21, 22.

Gavelinella pertusa (Marsson)

Plate 56, figs. 7–9

1878 *Discorbina pertusa* Marsson, p. 166, pl. 4, fig. 35*a–e*.
1891 *?Rosalina ammonoides* Reuss; Beissel (*non* Reuss), p. 74, pl. 16, figs. 1–4.
1925 *Anomalina pertusa* (Marsson); Franke, p. 86, pl. 7, fig. 16.
1928 *Anomalina pertusa* (Marsson); Franke, p. 182, pl. 17, fig. 4.

1932 *Anomalina pertusa* (Marsson); Cushman, p. 345, pl. 51, fig. 15*a*, *b*.
1941 *Discorbis lorneiana* (d'Orbigny) *pertusa* (Marsson); Marie, p. 217, pl. 34, fig. 316*a–c*.
1942 *Gavelinella pertusa* (Marsson); Brotzen, pp. 41–43, pl. 1, figs. 1, 2.
1942 *Gavelinella costata* Brotzen, pp. 43–45, pl. 1, fig. 3.
1953 *Gavelinella pertusa* (Marsson); Banner, pp. 46–49, pl. 10, fig. 3*a–c*.
1961 *Gavelinella pertusa* (Marsson); Barr, pp. 314–316, pl. 20, figs. 2, 3.

Remarks. Brotzen (1942, p. 41) stated that the septal ridges are not always well-defined, but are generally broad and flat, resembling chamber elevations, hence the number of chambers is not always easy to recognize. Brotzen differentiated between *G. costata* and *G. pertusa* by the possession of well-defined septal ridges in all examples of *G. costata*; these ridges are absent or weakly defined in *G. pertusa*. The latter form may show the development of a boss in the centre of the spiral side of the test. In the type description for *Discorbina pertusa*, Marsson (1978, p. 166) stated that the chambers are separated by weak sutures. Although no statement was made within the type description relating to the number of chambers present in the final whorl, Marsson's figure 35*b* illustrated the presence of fourteen chambers, whereas figures 35*a* and 35*d* showed only twelve chambers. All specimens identified as *G. pertusa* by the writer possess ten to eleven chambers in the final whorl, together with well-defined septal ridges; this observation is in agreement with Banner (1953, unpublished Ph.D. thesis) and Barr (1961, unpublished Ph.D. thesis), who stated that the presence of a smaller number of chambers than in the holotype falls within the limits of species variation. The majority of the specimens examined by the writer are small, flatly trochoid forms of the kind most often illustrated in the literature. Larger forms are more trochoid due to rapid increase in the size and thickness of the last-formed chambers. Pronounced flattening of the septal ridges, giving the appearance of weaker ridges, and a greater number of chambers, was observed in specimens at all levels within the stratigraphic range of *G. pertusa*. The differences between *G. costata* and *G. pertusa* as outlined by Brotzen (*op. cit.*) are a function of the degree of flattening of the septal ridge elements. No transitional forms were identified during the present study. Hence, the author employs the senior name of *G. pertusa* and regards *G. costata* as being synonymous.

Stratigraphic range. Basal *M. coranguinum* zone to the top of the *B. mucronata* zone.

Localities. Recorded in all the sections studied.

EXPLANATION OF PLATE 56

S.E.M. photographs.

Figs. 1–5. *Gavelinella lorneiana* (d'Orbigny) *sensu stricto*, BM P50801, 1, dorsal view; 2, ventral view; 3, edge view; 4, 5, edge and ventral views of form showing a greater degree of inflation of the final chamber, *M. coranguinum* zone, Faircross sub-surface section (I.G.S. index 557), Berkshire, southern England, × 70.

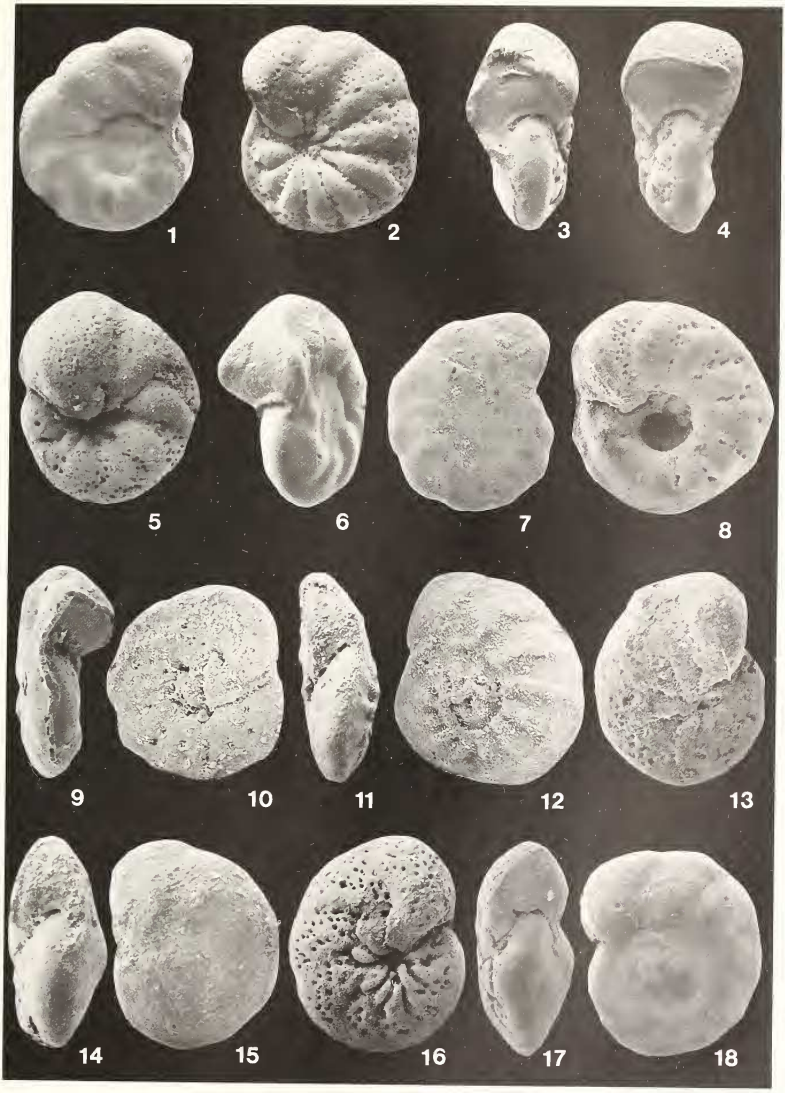
Fig. 6. *Gavelinella lorneiana* (d'Orbigny) var. *A*, BM P50802, edge view showing lateral elongations flanking the apertural face, *M. coranguinum* zone, Faircross sub-surface section (I.G.S. index 557), Berkshire, southern England, × 80.

Figs. 7–9. *Gavelinella pertusa* (Marsson), BM P50803, 7, dorsal view; 8, ventral view; 9, edge view, *B. langei* sub-zone, *B. mucronata* zone, West Runton, north Norfolk coast, East Anglia, × 80.

Figs. 10–12. *Gavelinella schloenbachi* (Reuss), BM P50804, 10, ventral view; 11, edge view; 12, dorsal view, upper *B. mucronata* zone, Mours, northern France, × 150.

Figs. 13–15. *Gavelinella praeinfrasantonica* (Vassilenko and Myatliuk), BM P50810, 13, ventral view; 14, edge view; 15, dorsal view, basal *M. coranguinum* zone, Faircross sub-surface section (I.G.S. index 557), Berkshire, southern England, × 120.

Figs. 16–18. *Gavelinella vombensis* (Brotzen), BM P50811, 16, ventral view; 17, edge view; 18, dorsal view, *M. coranguinum* zone, Winchester bypass section, Hampshire, southern England, × 70.



EDWARDS, *Gavelinella*

Gavelinella praeinfrasantonica (Vassilenko and Myatliuk)

Plate 56, figs. 13–15

1947 *Anomalina praeinfrasantonica* Vassilenko and Myatliuk, p. 211.

Remarks. This species, in its general morphology, is very close to *A. infrasantonica* Balakhmatova (assigned to *G. vombensis* by the present author), but it is distinguished from the latter by its smaller dimensions, the weakly expressed dorsal disc/boss, and the considerably less distinct stellate process. This species is the transitional form in the proposed evolution of *G. vombensis* (Brotzen) from the *Gavelinella schloenbachi* (Reuss) ancestral stock.

Stratigraphic range. Turonian to Coniacian (basal *Micraster coranguinum* (zone)).

Localities. 2, 10, 11, 12, 16, 17.

Gavelinella pseudoexcolata (Kalinin)

Plate 57, figs. 4–8

1937 *Anomalina pseudoexcolata* Kalinin, pp. 52; 60, pl. 6, figs. 97–99; pl. 7, figs. 100–102.
1957 *Gavelinella clementiana* (d'Orbigny) var. *thalmanni* (Brotzen); Hofker, pp. 295–296, text-fig. 351*a–d*.
1960 *Gavelinella pseudoexcolata* (Kalinin); Hiltermann and Koch pp. 320–321, pl. 48, figs. 3–4.
1962 *Pseudovalvulineria cristata* Goel, p. 192, pl. 12, fig. 1*a–c*.
1962 *Pseudovalvulineria hofkeri* Goel, p. 200, pl. 14, fig. 1*a–c*.

Remarks. The typical ornament on the spiral side of the planoconvex test consists of ridges, branches, and nodes, which are limited, in adult specimens, to the central area of the dorsal side. In juvenile specimens, the inflated, overlapping adult chambers are missing, and the test acquires a flattened dish-shape, similar to that of *Stensioina exsculpta exsculpta* (Reuss)

The new species erected by Goel (1962, 1965) and assigned to the genus *Pseudovalvulineria* are herein regarded as being synonymous with *G. pseudoexcolata*, and represent individuals showing various stages in the development of the dorsal ornamentation.

Stratigraphic range. Uppermost part of the *M. coranguinum* zone (basal Santonian) to the basal part of the *Gonioteuthis quadrata* zone.

Localities. 2, 5, 6, 7, 9, 13, 19.

EXPLANATION OF PLATE 57

S.E.M. photographs.

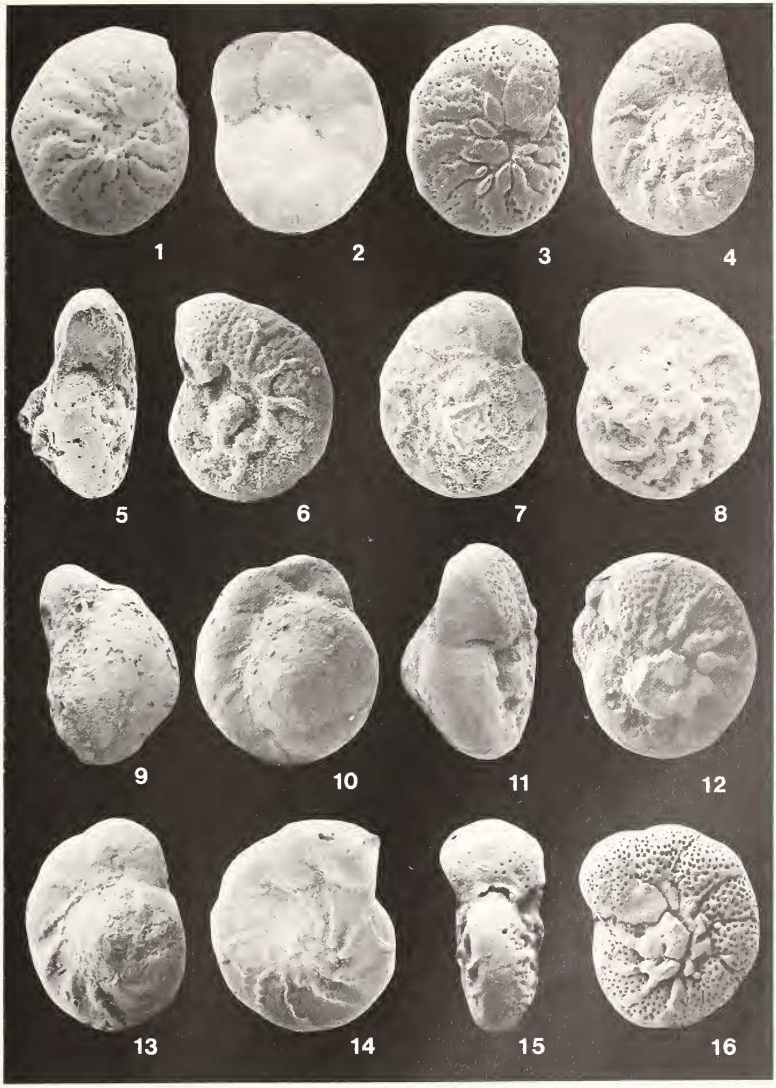
Figs. 1–3. *Gavelinella vombensis* (Brotzen), U.C.L. 300, 301, 1, 2, ventral and dorsal view of late form, upper *M. coranguinum* zone, Faircross subsurface section (I.G.S. index 557), Berkshire, southern England, × 70; 3, ventral view of form showing the stellate ornament around the umbilicus, *M. coranguinum* zone, Winchester Bypass section, Hampshire, southern England, × 80.

Figs. 4–8. *Gavelinella pseudoexcolata* (Kalinin), 4–6, BM P50807, 4, dorsal view; 5, edge view; 6, ventral view, early form, *M. coranguinum–M. socialis* zonal junction, Culver Cliff, Isle of Wight, × 90; 7, U.C.L. 302, dorsal view, showing increased test size and bundling of costae, base of *O. pilula* zone, Culver Cliff, × 70; 8, BM P50808, dorsal view of late form, *O. pilula–G. quadrata* zonal junction, Culver Cliff, × 60.

Figs. 9, 13. *Gavelinella clementiana convexa* n. ssp., paratypes, 9, BM P50797, edge view of extreme form showing pronounced convexity of the dorsal surface, (poorly preserved) lower *B. mucronata* zone, Farlington Redoubt, Hampshire, southern England, × 55; 13, BM P50796, form showing reduced dorsal calcite mass, lower *G. quadrata* zone, Culver Cliff, Isle of Wight, × 80.

Figs. 10–12. *Gavelinella clementiana convexa* n.ssp., holotype, BM P50795, 10, dorsal view; 11, edge view; 12, ventral view, *G. quadrata* zone, Pit 1067 (Brydone 1912), Hampshire, × 70.

Figs. 14–16. *Gavelinella clementiana costata* (Marie), BM P50798, 14, dorsal view; 15, edge view; 16, ventral view lower *B. mucronata* zone, locality 1 km. SSE of Broyes, Sézanne, northern France, × 55.



EDWARDS, *Gavelinella*

Gavelinella schloenbachi (Reuss)

Plate 56, figs. 10–12

1862 *Rotalia schloenbachi* Reuss, p. 84, pl. 10, fig. 5.
1935 *Anomalina schloenbachi* (Reuss); Keller, p. 553, pl. 3, figs. 22–24.
1947 *Planulina schloenbachi* (Reuss) var. *kelleri* Vassilenko and Myatliuk, p. 212, pl. 3, fig. 10*a–c*.
1947 *Planulina schloenbachi* (Reuss) var. *kalinini* Vassilenko and Myatliuk, p. 213, pl. 3, fig. 9*a–c*.

Remarks. Vassilenko and Myatliuk (1947) differentiated between *Anomalina* (*Rotalia*) *schloenbachi* (Reuss) from the Upper Albian, and *Anomalina* (*planulina*) *schloenbachi* (Reuss) var. *kelleri* Vassilenko and Myatliuk on the basis of the presence of a small disc in the centre of the dorsal side of the test. Furthermore, these workers separated the varieties *A. schloenbachi* var. *kelleri* and *A. schloenbachi* var. *kalinini* on the absence of the disc, and of the more distinct stellate sculpture in the latter form. The present author emphasizes that the study of other species groups reveals that the central disc or boss is subject to considerable variability. The morphology of the test of *G. schloenbachi* is seen to be highly variable within the limits of this species. The presence or absence of morphological features outlined by Vassilenko and Myatliuk in establishing variants of this species are not, in the writer's opinion, as stratigraphically clear-cut as the Russian workers suggested, hence, no sub-specific division is employed herein. The plasticity of the morphological characters in *G. schloenbachi* appears to have given rise to a number of evolutionary lineages. During the present study, individuals displaying inflated final chambers and more prominent septal ridges were noted at a number of levels within the Senonian, whereas Vassilenko and Myatliuk record these features as being characteristic of Lower Campanian representatives of this species. All the individuals of *G. schloenbachi* examined by the writer are small (0·3 to 0·4 mm in diameter), and are only retained on the 75 μm mesh during sieving of the residues, being absent from the coarser fractions.

Stratigraphic range. *G. schloenbachi* ranges throughout the Senonian interval, and it is also recorded in the Albian by other workers. This species is a consistent component of the 'background fauna' in the foraminiferal assemblages studied, generally occurring in relatively low abundances. However, sporadic increases in the percentage totals of this species occur at the base of the Santonian and again at the base of the Campanian in southern England. These stratigraphic levels coincide with the first appearances of a number of new gavelinellid species.

Localities. Recorded in all sections studied.

EXPLANATION OF PLATE 58

S.E.M. photographs.

Figs. 1, 2. *Gavelinella clementiana costata* (Marie), U.C.L. 303, 304, 1, ventral view showing reduced umbilical thickening of costae, × 50; 2, dorsal view of late form × 50, *B. mucronata* zone, Mours, northern France.

Figs. 3–5. *Gavelinella clementiana clementiana* (d'Orbigny), BM P50800, 3, ventral view; 4, dorsal view; 5, edge view; *B. langei* sub-zone, *B. mucronata* zone, West Runton, north Norfolk Coast, East Anglia, × 50.

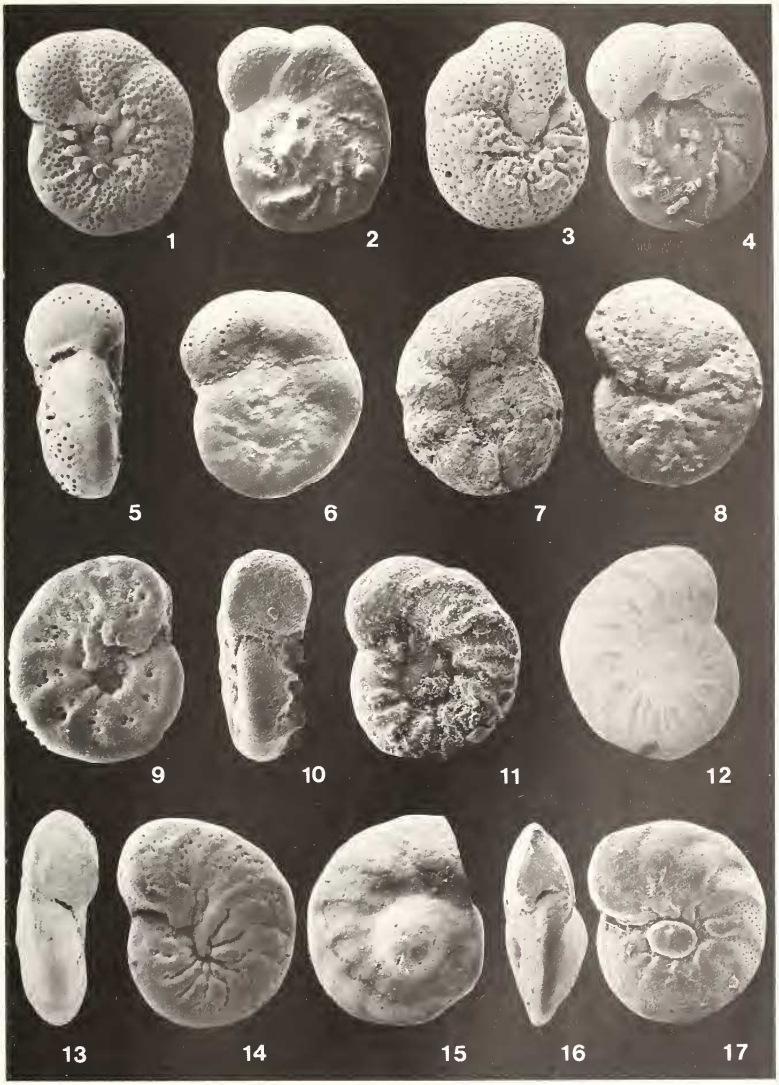
Fig. 6. *Gavelinella clementiana laevigata* (Marie), BM P50799, dorsal view, *B. langei* sub-zone, *B. mucronata* zone, Sheringham, north Norfolk Coast, East Anglia, × 50.

Figs. 7, 8. *Gavelinella thalmanni* (Brotzen), BM P50806, 7, dorsal view; 8, ventral view, early form, *M. cortestudinarium* zone, Faircross sub-surface section (I.G.S. index 557), Berkshire, southern England, × 150.

Figs. 9–11. *Gavelinella thalmanni* (Brotzen), BM P50805, 9, ventral view; 10, edge view; 11, dorsal view, *G. quadrata* zone, Farlington Redoubt, Hampshire, southern England, × 120.

Figs. 12–14. *Gavelinella stelligera* (Marie), BM P50812, 12, dorsal view; 13, edge view; 14, ventral view, *M. coranguinum* zone, Faircross subsurface section (I.G.S. index 557), Berkshire, southern England, × 80.

Figs. 15–17. *Gavelinella monterelensis* (Marie), BM P50813, 15, dorsal view; 16, edge view; 17, ventral view, lower *B. mucronata* zone, locality 1 km. SE of St. Nicholas le Chapelle, Provins, northern France, × 80.



EDWARDS, *Gavelinella*

Gavelinella stelligera (Marie)

Plate 58, figs. 12–14

1941 *Planulina stelligera* Marie, p. 245, pl. 37, fig. 344*a–c*.
1963 *Anomalina* (*Pseudovalvulineria*) *stelligera* (Marie); Kaptarenko-Chernousova *et al.*, pl. xx, fig. 5*a–c*.

Remarks. This species is characterized by the strongly compressed nature of the test, with twelve to thirteen chambers in the final whorl, and by the stellate arrangement of plates around the ventral umbo.

Stratigraphic range. *G. stelligera* has been recorded from the Upper Santonian to the Lower Campanian of the Ukraine and the Russian platform; the Santonian of the Crimea and the north Caucasus region, and from the Campanian of France. The present author cites the stratigraphic range of this species as from the uppermost part of the *M. coranguinum* zone to the base of the *B. minor* sub-zone (*B. mucronata* zone).

Localities. 1, 2, 3, 4, 5, 6, 7, 9, 11, 13, 14, 18, 19, 21.

Gavelinella thalmanni (Brotzen)

Plate 58, figs. 7–11

1936 *Cibicides thalmanni* Brotzen, pp. 190–191, pl. 4, fig. 7*a–c*.
1956 *Anomalina* (*Gavelinella*) *sculptilis* Hiltermann and Koch, p. 38, pl. 3, fig. 3.
1961 *Gavelinella thalmanni* (Brotzen); Barr, pp. 316–318, pl. 21, figs. 4, 5.
1962 *Gavelinella sculptilis* Hiltermann and Koch; Hiltermann and Koch, p. 319, pl. 48, fig. 2.
1977 *Gavelinella thalmanni* (Brotzen); Koch, p. 41, pl. 2, figs. 1–3.

Remarks. This small, cosmopolitan species has a characteristically strongly umbilicate test, and gently curved septal ridges of opaque shell material merging into a thickened carinal band. *G. thalmanni* is readily distinguishable from other gavelinellid species in possessing a strongly developed dorsal umbilicus. The early dorsal whorls are apparent in the majority of the specimens studied whereas the type figure for this species displays a deeply situated umbilical disc.

Stratigraphic range. Lower to mid part of the *Micraster cortesudinarium* zone to the uppermost part of the *B. mucronata* zone.

Localities. Recorded in all sections studied.

Gavelinella vombensis (Brotzen)

Plate 56, figs. 16–18; Plate 57, figs. 1–3

1940 *Anomalina clementiana* (d'Orbigny); Cushman, p. 29, pl. vii, (*non* pl. v), figs. 7*a–c*.
1945 *Pseudovalvulineria vombensis* Brotzen, pp. 50–51, pl. 1, figs. 12, 13 (*non* fig. 9, 1–4).
1963 *Anomalina* (*Pseudovalvulineria*) *infrasantonica* (Balakhmatova); Kaptarenko-Chernousova, pl. xx, fig. 4*a–c*.

Remarks. The principal distinguishing feature of *G. vombensis* is the stellate pattern of thread-like depressions of varying length encircling the ventral umbilicus, as described by Brotzen (1944). Adult tests are biconvex, planispiral, with ten to twelve chambers in the final whorl. On the dorsal/spiral side of the test, the inner whorls are covered by a smooth, convex boss of variable size in the majority of the specimens examined. This boss is present in all growth stages.

The inclusion of *Rotalia beccariiformis* White, 1928 into Brotzen's synonymy for *Pseudovalvulineria vombensis* (Brotzen 1944, pl. 1, fig. 5) is, in the writers opinion, incorrect. *Rotalia beccariiformis* may be distinguished from *G. vombensis* on the basis of the following morphological differences: (*a*) the absence of a dorsal boss; (*b*) the depressed sutures on the ventral side of the test are divided into beads near the umbilicus.

The specimens figured by Brotzen (*op. cit.*, p. 50, text-fig. 9, 1–4), from the Lower Campanian, appear to lack the circle of thread-like depressions herein regarded as being definitive of the species. These specimens display a swelling of the proximal ends of the ventral septal ridges, and their projection into the umbilicus, and appear to be more closely analogous to specimens identified as *Gavelinella clementiana convexa* n. ssp. by the present author. Therefore *G. vombensis* (Brotzen) *sensu stricto* has a more restricted stratigraphic range than initially outlined by Brotzen (*op. cit.*). *G. vombensis* and *A. infrasantonica* (Balakhmatova) are synonymous, in the authors opinion, on the basis of the morphological features outlined, and on the understanding that Russian workers include the *M. coranguinum* zone within the Santonian stage.

Stratigraphic range. Upper part of the *M. cortestudinarium* zone to the upper part of the *M. coranguinum* zone.

Localities. 2, 8, 10, 11, 12, 15, 16, 17.

EVOLUTIONARY INTERPRETATION

In the light of the results obtained from the present study the author suggests that a plexus of evolving forms, included within the genus *Gavelinella* during the Senonian interval, were derived from two separate ancestral stocks:

1. The *Gavelinella ammonoides* (Reuss) stock in the Turonian.
2. The long-ranging *G. schloenbachi* stock throughout the Turonian and Senonian.

1. The evolution of forms arising from the *G. ammonoides* root stock.

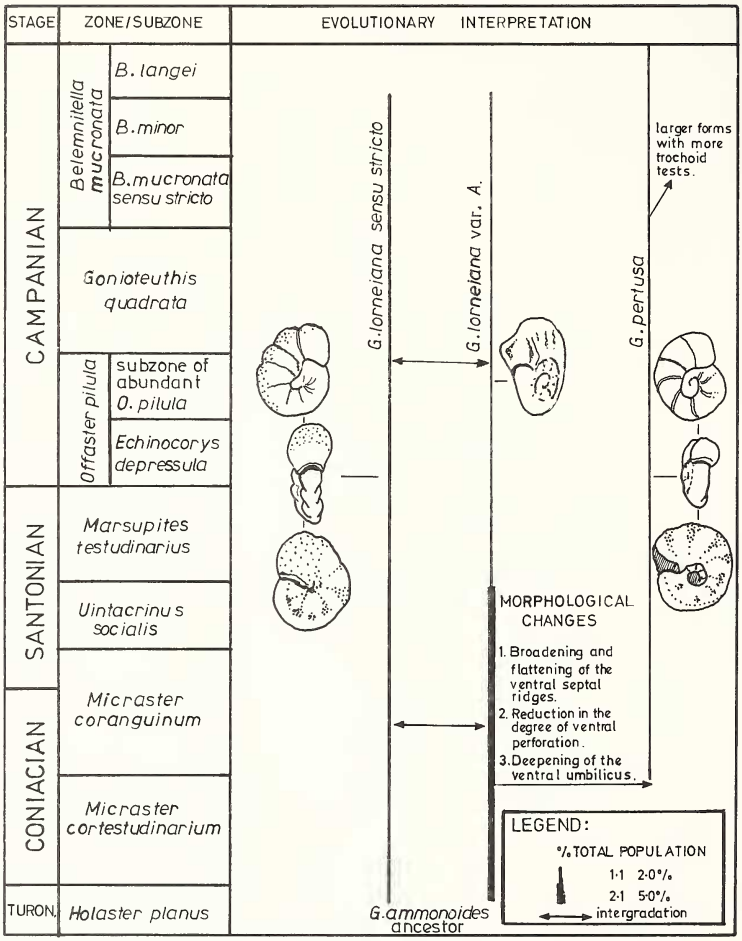
The *G. ammonoides–G. costata–G. pertusa* evolutionary lineage outlined by Brotzen (1942) now requires some modification. *G. costata* and *G. pertusa* are herein regarded as being synonymous. Many similarities exist in the test morphologies of *G. lorneiana* and *G. pertusa* suggesting that there is a genetic affinity between them. The writer proposes that *G. pertusa* evolved from the longer-ranging *G. lorneiana* stock which itself arose from a *G. ammonoides* ancestor within the Turonian (Brotzen 1942; Vaptzarova 1970). The evolutionary changes involved in the transition from *G. lorneiana* to *G. pertusa* are threefold:

(*a*) The formation of a deeper, incompletely enclosed, broad-sided umbilicus from forms with a narrow, shallow umbilicus. Observations carried out on numerous representatives of *G. lorneiana* reveal a variation in the degree of coiling of the test. Forms in which the coiling is more openly helical appear to have given rise to the deep umbilicus seen in *G. pertusa*.

(*b*) Broadening and flattening of the septal ridges which run along the anterior margin of each chamber on the ventral side of the test. Hence the ridges become less distinct and resemble chamber elevations.

(*c*) Reduction in the number of pores on the ventral side of the test. Marsson (1878, p. 166) described the type specimen of *G. pertusa* as bearing very few, fairly large, scattered pores on the ventral surface. In the writer's interpretation, these scattered pores represent relicts of the coarse perforation observed on the ventral side of the test of the postulated *G. lorneiana* ancestor. The broadening and flattening out of the imperforate septal ridges reduced the surface area of the interspersed perforate portions of the test (text-fig. 2). These pores are more widespread between the narrower septal ridges that divide the final two or three chambers in *G. pertusa* (Pl. 56, fig. 8).

The weak lateral elongations flanking the apertural face, together with the presence of a septal ridge between the last two chambers in specimens of *G. pertusa* indicate derivation from *G. lorneiana* var. A rather than from *G. lorneiana sensu stricto*. In specimens of the latter from the final chamber is more inflated, and the suture between the last two chambers is marked by a narrow depression only.



TEXT-FIG. 2. The evolutionary interpretation of the *Gavelinella lorneiana–G. pertusa* lineage.

2. The evolution of forms arising from the *G. schloenbachi* root stock.

Representatives of *G. schloenbachi* were observed throughout the Senonian interval, and are suggested to comprise the root stock from which a number of evolutionary lineages subsequently arose.

(*a*) The *G. schloenbachi–G. praeinfrasantonica–G. vombensis* evolutionary lineage (text-fig. 3). Vassilenko and Myatliuk (1947) recognized a genetic relationship between *G. schloenbachi* and *G. praeinfrasantonica* as evidenced by the similarity in the structure of the dorsal test surface, i.e. the presence of a weakly expressed disc. This latter feature is, in fact, highly variable both in size and presence.

It is probable that *G. praeinfrasantonica* evolved during the Turonian from a *G. schloenbachi* ancestor bearing a weak dorsal umbilical disc. The course of evolution would necessitate an increase in the size and the biconvexity of the test, and the increased prominence of the dorsal septal ridges.

Within the upper part of the *M. cortestudinarium* zone in the Faircross and Winterbourne sub-surface sections a complete transition was observed from *G. praeinfrasantonica* to *G. vombensis* (*Anomalina infrasantonica* of Russian workers). Morphological changes involved in this transition are: (*a*) the continued increase in the dimensions of the test and (*b*) the enhancement of the stellate pattern of thread-like depressions encircling the ventral umbilicus.

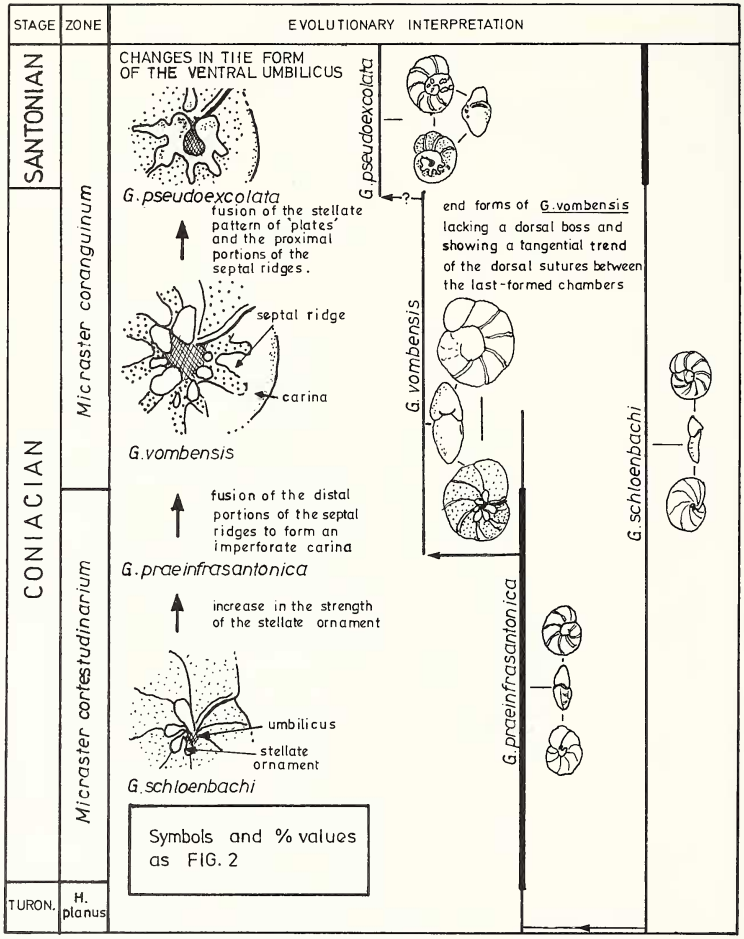
(*b*) The possible evolution of *G. pseudoexcolata* from *G. vombensis* (text-fig. 3).

G. pseudoexcolata is first recorded in the uppermost horizons of the *M. coranguinum* zone in the Culver Cliff and Faircross sections and in the equivalent lower *M. coranguinum* zone of French stratigraphers. However, its evolutionary origin is uncertain. Vaptzarova (1970) indicated that this species evolved from the *G. thalmanni* stock comprising individuals possessing flatly trochoid, nearly planispiral tests which are strongly umbilicate with prominent dorsal septal ridges. During the course of the present study the author did not observe any forms that were transitional between *G. thalmanni* and *G. pseudoexcolata*. Alternatively the writer suggests that the origins of the latter species lie within the *G. vombensis* stock. Certain individuals of *G. vombensis* lacking the dorsal boss, and possessing prominent ventral septal ridges were observed towards the end of the stratigraphic range of this species in the Faircross section, seemingly heralding the first appearance of *G. pseudoexcolata*. Certain morphological features of the test are shared by both species, i.e. a planispiral, dorsally concave test, with a coarsely perforate ventral surface. The ventral septal ridges flatten distally and merge into a thickened carinal band in both species. The distinct stellate ornament encircling the ventral umbilicus in *G. vombensis*, in detail, consists of slightly raised, imperforate plates, and their fusion may be envisaged as forming the umbilical thickening observed in *G. pseudoexcolata*, although no intermediate stages were observed during the present study. The characteristic tangential orientation of the dorsal septal ridges between the last chambers in *G. pseudoexcolata* was also observed in the final sutures of end forms of *G. vombensis*.

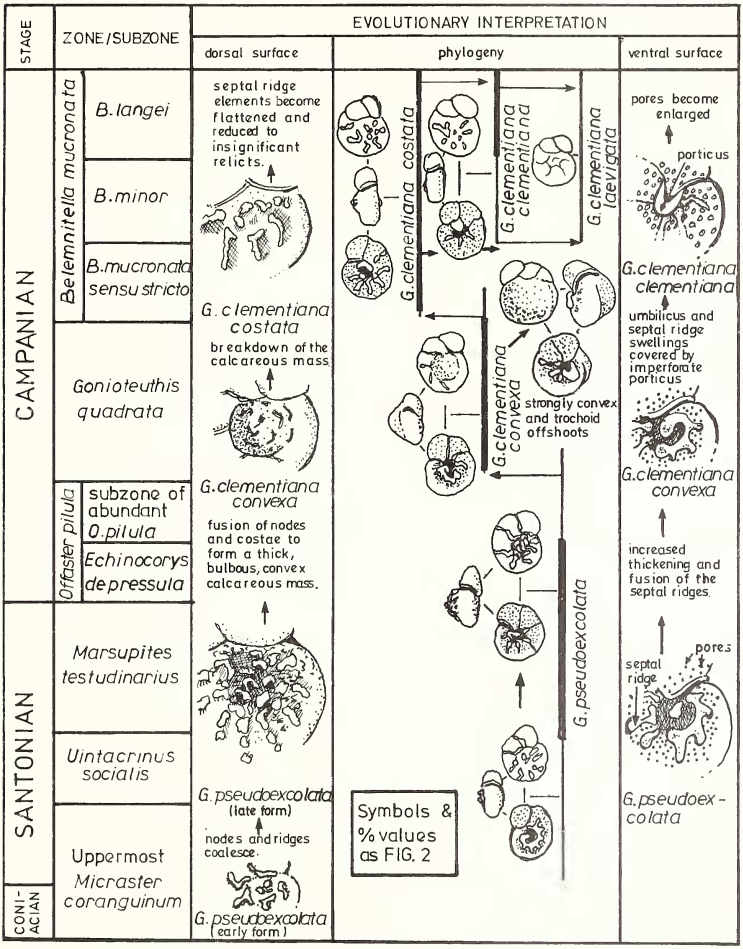
(*c*) The *G. pseudoexcolata–G. clementiana* evolutionary lineage (text-fig. 4).

In the author's opinion, there is a total gradation from *G. pseudoexcolata* through *G. clementiana convexa* to *G. clementiana clementiana*. This observation is in agreement with the findings of Hiltermann and Koch (1960). The typical dorsal ornament of *G. pseudoexcolata* consists of branches of the septal ridge elements which become more irregular and detached into translucent nodes with time. These nodes and ridges are strongly raised in the central area. The depression along the spiral suture becomes granular in appearance, and the central ornament develops into an irregular mass of costae (Pl. 57, fig. 8). Individuals displaying such an ornamentation dorsally are characteristic of the *Offaster pilula* zone.

The first appearance of *G. clementiana convexa* is marked at the base of the *Gonioteuthis quadrata* zone by the presence of individuals showing increased convexity of the dorsal surface of their tests resulting from the fusion of the costae and nodes, seen in *G. pseudoexcolata*, to form a bulbous calcareous mass of variable size (Pl. 57, fig. 10). On the ventral side of the test



TEXT-FIG. 3. The evolutionary interpretation of the *Gavelinella schloenbachi*–*G. praeinfrasantonica*–*G. vombensis*–*G. pseudoexcolata* lineage.



TEXT-FIG. 4. The evolutionary interpretation of the *Gavelinella pseudoexcolata–G. clementiana* lineage.

there is increased thickening and fusion of the septal ridges in the umbilical area. The third trend of evolution is the development of a more pronounced marginal, imperforate rim or carina, by the flattening of the distal extremities of the clear septal ridges between the early chambers. The coarse perforation of the test wall is well preserved between the septal ridges in the umbilical region (Pl. 57, fig. 12). In individuals of *G. clementiana convexa* in which the central, dorsal mass is reduced in size, the depressed spiral suture becomes evident, again showing granulation.

In the lower *B. mucronata* zone in the Farlington Redoubt and Culver Cliff sections, rare, strongly convex, trochoid forms are seen to diverge from the *G. clementiana convexa* stock. These individuals are large, and show pronounced thickening of the shell material ventrally together with extreme convexity of the dorsal calcitic mass (Pl. 57, fig. 9). These forms appear to be synonymous with the species identified as *Pseudovalvulineria trochus* by Goel (1965).

Also at the base of the *B. mucronata* zone appear individuals of *G. clementiana convexa* displaying the breakdown of the dorsal calcareous mass and the redevelopment of central nodes and ridges. There is also a reduction in the width of the imperforate margin, and in the degree of ventral umbilical thickening in these individuals. These latter forms mark the transition to *G. clementiana costata*.

Therefore, the lower horizons of the *B. mucronata* zone are defined by assemblages containing *G. clementiana convexa*, together with rare, extreme, trochoid forms of this subspecies marking the maximum development of the morphological features outlined, and *G. clementiana costata*. *G. clementiana convexa* gradually disappears from the fauna by continuous gradation into the *costata* subspecies.

Further reduction in the strength of the dorsal septal ridge elements, and in the degree of ventral umbilical thickening, together with the disappearance of the imperforate margin in derivatives of the *G. clementiana costata* stock within the *B. minor* sub-zone, give rise to forms corresponding to the typical *G. clementiana* of d'Orbigny (1840). Imperforate portici cover the ventral umbilicus in well-preserved specimens of *G. clementiana clementiana*. There is also an enlargement of the diameters of the pores which cover the ventral surface of the test. The degree of inflation of the final chamber is subject to variation.

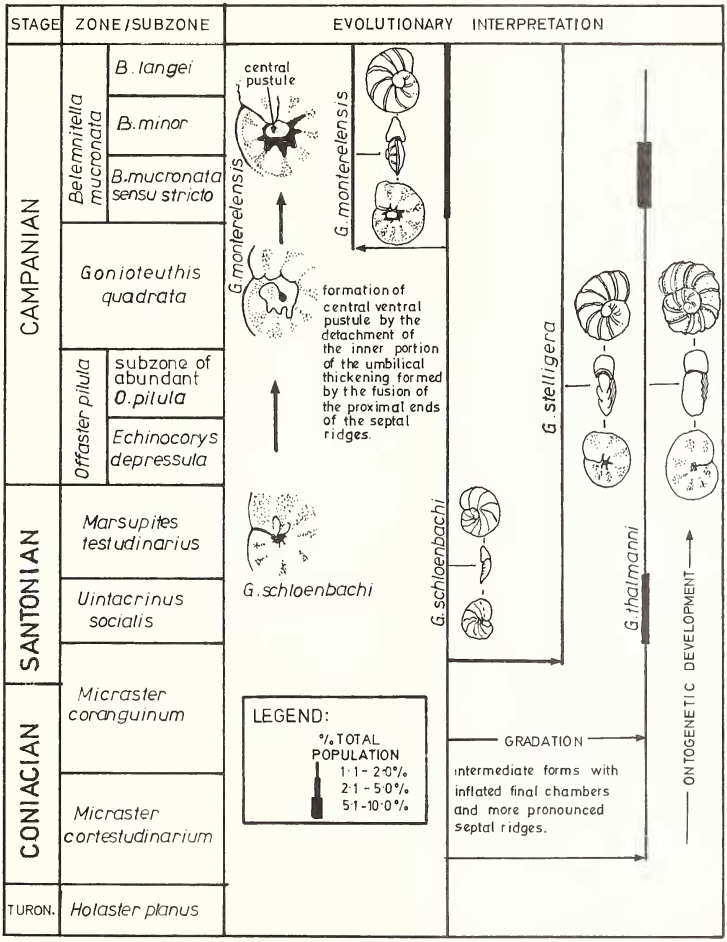
Within the *G. clementiana* plexus, the dorsal septal ridges become progressively reduced with time, until they are no more than insignificant relicts in the *B. minor* and *B. langei* sub-zones. Individuals showing the unornamented state of the dorsal surface of the test are analogous with the *laevigata* variety of Marie (1941) which is herein given a subspecific status. Although individuals corresponding to the *rugosa* variety of Marie (1941, pl. 33, fig. 312*a–c*) were not observed during the present study the morphological characters of the test of that variant as described by Marie may be envisaged as having developed from the *G. clementiana costata* stock through the breakup of the dorsal ornamentation.

(*d*) The *G. schloenbachi–G. thalmanni* evolutionary lineage (text-fig. 5).

G. thalmanni was first recorded within the lower part of the *M. cortestudinarium* zone and appears to have evolved directly from the *G. schloenbachi* root stock. Transitional forms were noted at this stratigraphic level, as well as at other horizons higher in the Senonian, suggesting that morphological gradation continues throughout as well as the natural course of ontogenetic development within the species *G. thalmanni*. The transitional forms (Pl. 58, figs. 7, 8) are distinguished from the ancestral *G. schloenbachi* by the more pronounced dorsal septal ridges, the inflated final chambers, and the disappearance of the weak stellate structure around the ventral umbilicus. Continued enlargement of the gently curved dorsal septal ridges, an increase in the test dimensions, and the development of a strong dorsal umbilicus mark the onset of *G. thalmanni sensu stricto*.

(*e*) The *G. schloenbachi–G. stelligera* evolutionary lineage (text-fig. 5).

The writer is in agreement with Vaptzarova (1970) in proposing the derivation of *G. stelligera* from a *G. schloenbachi* ancestor. *G. stelligera* is distinguished from the latter



TEXT-FIG. 5. The suggested evolution of *Gavelinella thalmanni*, *G. stelligera*, and *G. monterelensis* from the *G. schloenbachi* root stock.

species by the greater dimensions (0·6 mm diam.), the more prominent marginal keel, the shallower ventral umbilicus, and by the greater prominence of the stellate ornament around the umbilicus. Very few morphological changes took place during the course of evolution of *G. stelligera* from *G. schloenbachi*, the development of the former species taking the form of enhancement of features already present in the test morphology of the ancestor.

(*f*) The *G. schloenbachi–G. monterelensis* evolutionary lineage (text-fig. 5).

The origin of *G. monterelensis* within the upper part of the *G. quadrata* zone is uncertain. Vaptzarova (op. cit.) suggested *Anomalina* (*Brotzenella*) *tendami* to be the ancestral form; however, no representatives of the latter species were recorded during the present study. The writer tentatively suggests that *G. monterelensis*, with its compressed, planispiral test and keeled periphery, evolved from a *G. schloenbachi* ancestor bearing a weak dorsal disc which developed into the convex central boss of the former species. The proposed course of evolution necessitates an increase in the chamber number (12 to 13); increased perforation of the ventral test surface; swelling of the proximal extremities of the ventral septal ridges and their ultimate fusion to form an umbilical thickening. The innermost, umbilical, portion of the spiral thickening becomes detached to form the central pustule seen in certain individuals of *G. monterelensis*.

CONCLUSIONS

The structural types comprising the various lineages described became established primarily as a result of morphological variations within the ancestral species *G. schloenbachi*. It is clear that certain structural types evolved separately from distinct lineages, e.g. *G. monterelensis* shows the development of ventral umbilical thickening of imperforate shell material together with coarse ventral wall perforation, which are also seen in the species *G. pseudoexcolata* and *G. clementiana*. The relatively higher degree of variation within the genus *Gavelinella* during the Campanian may be attributed to lower selection pressures, resulting from a combination of physical and biological factors. This increase in variation corresponds to the greater degree of faunal diversity noted within the Campanian stage. On the basis of results obtained from a study of various foraminiferal faunal parameters (Edwards, 1979, unpublished Ph.D. thesis) the writer interprets the environmental conditions which prevailed during the Senonian interval in north-west Europe to have been of a predominantly stable, normal marine, continental shelf character. Such environmental stability negates the consideration of the role of marked changes in any major environmental factor such as temperature, salinity, etc., in influencing the evolution of the morphocharacters described. Indeed, no precise explanation of why the evolution took place can be put forward at the present state of knowledge. However, changes in the depth of the Senonian seas can be shown to have certain effect upon the nature of the gavelinellid test morphology. Koch (1977, p. 46) noted that large specimens of the species *G. pseudoexcolata* with an inflated and overlapping final chamber were indicative of shallow water, littoral habitats in the Senonian sequences of northern Germany. Away from the shore, individuals of this species were less frequent, smaller, and lacked the inflated chamber. The present author observed the latter morphological state in individuals of *G. pseudoexcolata* throughout its entire range in the Anglo-Paris basin succession. Since test features are genetically linked characters, their evolution may be due partly to a basic plan inherent within any one species or group of species. This would explain the coexistence of derivations of several evolutionary lineages within the same fossil assemblage, and the occurrence of complete evolutionary sequences in widely separate basins of deposition, e.g. the Anglo-Paris basin and north-west Bulgaria (Vaptzarova, op. cit.). However, the recorded occurrences of the gavelinellid species outlined are poorly defined owing to the differing morphological and nomenclatural interpretations proposed by various workers. It is therefore hoped that the observations made during this study will help clarify the phylogenetic relationships of the *Gavelinella* group during the Senonian.

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APPENDIX. LIST OF LOCALITIES AND HORIZONS FROM WHICH THE FORAMINIFERA STUDIED WERE OBTAINED

East Anglia

1. Coastal section between Weybourne Hope and Overstrand. (O.S. sheets (6 inch:1 mile) TG 14, SE, SW; TG 23, NE, N.G.R.: TG 111439 to TG 254406.) *Belemnitella minor* sub-zone and *B. langei* sub-zone (*B. mucronata* zone).

Southern England

2. Whitecliff Bay–Culver Cliff coastal section, 3·5 km south-east of Brading, the Isle of Wight (Hampshire). (O.S. sheet (6 inch:1 mile) SZ 68, NW, N.G.R.: SZ 650865 to SZ 638856.) Continuous section comprising all the zones of the Senonian.

3. Farlington Redoubt, 4 km west of Havant (Hampshire), (O.S. sheet (6 inch:1 mile) SU 60, NE, N.G.R.: SU 686065.) *Gonioteuthis quadrata* zone, lower *B. mucronata* zone.

4. Pit 1067, Brydone (1912), the more southern of two large quarries situated 1 km north-east of Mottisfont, Hampshire. (O.S. sheet (6 inch:1 mile) SU 32, NW, N.R.G.: SU 337275.) *Gonioteuthis quadrata* zone.

5. Pit 743, Brydone (op. cit.), Little Rye Farm, 1·2 km south-east of Odiham, Hampshire. (O.S. sheets (6 inch:1 mile) SU 75, SE, N.G.R.: SU 774499.) *Marsupites testudinarius* zone to lower *Offaster pilula* zone.

6. Pit 741, Brydone (op. cit.), Roke Farm, 2·2 km south-east of Odiham, Hampshire. (O.S. sheet (6 inch: 1 mile) SU 74, NE, N.G.R.: SU 762494.) *M. testudinarius* zone.

7. Pit 173, Brydone (op. cit.), 0·25 km south-west of Odiham, Hampshire. (O.S. sheet (6 inch:1 mile) SU 75, SW, N.G.R.: SU 737506.) Uppermost *Micraster coranguinum* zone, *Uintacrinus socialis* zone.

8. Section on the western side of the Winchester Bypass (A33T) (O.S. Sheet (6 inch:1 mile), SU 442, NE, N.G.R. SU 493293 to SU 493299.) *Micraster cortestudinarium* and *M. coranguinum* zones.

9. The Sussex coast—a cliff section stretching from Peacehaven, 1·2 km eastwards to Friar's Bay. (O.S. sheets (6 inch:1 mile) TQ 40, SW, TQ 30, SE, N.G.R.: TQ 411005 to TQ 425004.) Uppermost *M. testudinarius* zone, *O. pilula* and lowermost *G. quadrata* zone.

10. Winterbourne sub-surface section. Borehole number (I.G.S. index) 267/251a, 6·5 km. north-west of Newbury, Berkshire. (O.S. sheet (6 inch:1 mile) SU 47, SE, N.G.R.: SU 454716). *H. planus*, *M. cortestudinarium*, *M. coranguinum* zones.

11. Faircross sub-surface section. Borehole number (I.G.S. index) 268/557. Located 0·5 km north of Faircross, Berkshire. (O.S. sheet (6 inch:1 mile) SU 66, SE, N.G.R.: SU 697632.) *H. planus*, *M. cortestudinarium* zones.

NORTHERN FRANCE

12. Chalk pit 0·5 km south of the village of Villeneuve l'Archevèque, 10 km east of Sens. Upper *Micraster decipiens* zone (French zonal scheme) = middle to upper *M. coranguinum* zone (British zonal scheme).

13. Pit 400 m north, north-west of Foissy-sur-Vanne, 18 km east of Sons. Lower *M. coranguinum* zone (France) = upper *M. coranguinum* zone (Britain).

14. Small pit north, north-west of La Grenouillére, 10 km east of Sens. *M. decipiens* zone (France) = *M. coranguinum* zone (Britain).

15. Pit 2 km south of Les Sièges, 18 km east, south-east of Sens. *M. decipiens* zone (France) = lower *M. coranguinum* zone (Britain).

16. The westernmost of two chalk pits immediately to the north of Les Thorets, 12 km south-east of Sens. *M. decipiens* zone (France) = *M. coranguinum* zone (Britain).

17. Small disused pit, north-west of Vaumont, 2 km west of locality 16. Middle *M. decipiens* zone (France) = lowermost *M. coranguinum* zone (Britain).

18. Pit lying to the east of the D439 road to Thorigny-sur-Oise, at its junction with the D79 road to Sognes, 24 km south, south-east of Provins. Upper *Actinocamax quadratus* zone (France) = lower *G. quadrata* zone (Britain).

19. Small pit located to the north of the D116 road to St. Martin de Bossenay, 30 km south-east of Provins. Lower *A. quadratus* zone (France) = *O. pilula* zone (Britain).

20. Large, disused chalk-pit lying alongside the D40, a road to St. Nicholas-la-Chapelle, 12 km east, south-east of Provins. Lower *B. mucronata* zone.

21. Pit located 1 km south, south-east of Broyes, 2 km north-east of Sézanne. Lower *B. mucronata* zone.

22. Disused quarry north-east of Mours, lying to the east of the D76 road at its junction with the main railway line. Upper *B. mucronata* zone.